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TRADE-OFFS AND CONSTRAINTS ON EASTERN KINGBIRD PARENTAL CARE

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ABSTRACT.—Ten Eastern Kingbird (*Tyrannus tyrannus*) nests were observed for 97 h to determine age-related changes in parental care and to identify possible trade-offs and constraints on feeding, brooding, and vigilant behavior. Feeding rate (trips/h) was related positively to nestling age and brood size, but related negatively to amount of time spent vigilant. Per capita nestling feeding rates (trips/nestling/h) were affected most strongly and negatively by brood size, precipitation, and time spent vigilant. Time spent brooding declined as nestlings aged and as air temperature rose, whereas the amount of time spent shading nestlings varied only (inversely) with cloud cover. Vigilance time averaged about 20% of each hour, was independent of age and brood size, but was related negatively to amount of time spent in nestling maintenance (brooding plus shading), the number of feeding trips made to nests, and nest visibility. Weather had major influences on feeding and brooding behaviors, but regardless of other factors, kingbirds appear to reserve time for vigilance. Parental behavior thus reflects the action of a large number of factors that require compromises in the apportionment of time to the feeding, maintenance, and protection of young. *Received 10 Sept. 1993, accepted 20 Feb. 1994.*

Parental behaviors, such as feeding rates, often change predictably over the course of the nesting cycle (Bedard and Meunier 1983, Moreno 1987), but considerable variation in parental behavior may result from the action of unpredictable environmental factors. Variation in parental care due to weather is often of great ecological significance, and only by documenting and identifying the causes of variation can its importance be appreciated (Johnson and Best 1982, Wittenberger 1982). Furthermore, studies of how parental behavior changes throughout the nesting cycle provides information as to whether trade-offs exist among parental behaviors (Breitwisch et al. 1986, Grundel 1987, Haggerty 1992) and when critical periods in development occur (Morehouse and Brewer 1968).

Eastern kingbirds (*Tyrannus tyrannus*) are single-brooded and normally lay a clutch of three or four eggs (Murphy 1983a, Blancher and Robertson 1985a). Predation is the major cause of nest mortality (Murphy 1983b, Blancher and Robertson 1985b), but low temperatures and/or precipitation have negative impacts on nestling growth and fledging success (Murphy 1983c, Hayes and Robertson 1989). Here we document major components of parental care vary with nestling age and brood size, identify environmental sources of variation in parental care, and describe trade-offs that exist among parental behaviors.

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STUDY AREA AND METHODS

We conducted this study during June and July 1989 in the Charlotte Valley, Delaware Co., New York. The main study area was near Hartwick College's Pine Lake Biological Field Station, between the towns of Davenport and West Davenport. Habitats within the area are mainly a mixture of pastures, hedgerows and riparian environments. See Bischoff and Murphy (1993) for a more complete description of the area. All nests were found prior to egg-laying and were followed closely until laying was complete. We therefore knew the true clutch size for each nest (6 clutches of 3 eggs, 3 of 4 eggs and 1 of 2 eggs). Due to the failure of some eggs to hatch, and our desire to maintain a distribution of brood sizes similar to the original clutch sizes, Murphy transferred one or two nestlings into several nests within 24 to 48 h after hatching. Nestlings within a brood never differed in age by more than one day. Our observations are based on data from five broods of three young, three broods of four, and two broods of two. Rosa was not informed of brood sizes or nestling ages in order to keep observations unbiased. Observations at (usually) trios of nests with nestlings of the same age alternated between morning (before 11:00 EST), midday (11:00 to 13:00 EST) and afternoon (after 13:00 EST) on successive days. Observations at the same nest are not statistically independent. Conceivably, nests on low or high quality territories or nests tended by pairs with different levels of experience might produce spurious results. We attempted to minimize this potential problem by making observations at each nest at different times of day and over a range of weather conditions. Each observation period (N = 43) was treated as a single observation, based on the two (sometimes three) hours over which Rosa collected data. Our analysis is thus based on 97 h of observations from 10 nests.

Parental behaviors were monitored either from a blind located about 30 m from the nest or from a parked vehicle at the edge of roads. Using binoculars, Rosa observed nests between days 2 and 14 of the nestling period (hatching = 1). She collected data on the number of feeding trips and time spent brooding, chasing predators, shading young, and being vigilant. We did not analyze chasing time because little time was spent on this behavior. Time of day was recorded as the midpoint of the observation period. We included several nest sites characteristics in the analysis, including height (meters above ground), distance from the canopy edge (meters), and shading on a scale of 0 (no shading) to 4 (complete cover). Weather variables monitored during the observation period included air temperature, wind speed, precipitation and cloud cover. Rosa recorded each variable 30 minutes after observations began and then at hourly intervals until the observation period ended. Air temperature was measured with a shaded mercury thermometer. Other weather variables were estimated on a scale of 0 to 4. Scores of 0 were given to each variable when no wind, rainfall, or cloud cover was present. Conversely, observation periods with strong winds, heavy precipitation, and complete cloud cover were assigned values of 4.

We defined brooding as occurring when the female settled down on the nest and covered the nestlings. Shading females stood over the nestlings with wings spread to shield them from the sum. Nest attendance was the total time spent brooding and shading young. We defined a vigilant bird to be one that perched attentively in the vicinity of the nest, scanned the area while its mate was away from the nest, and did not feed either itself or the nestlings. Given that the birds were not individually marked, we did not attempt to separate feeding trips according to sex of the parent.

With the exception of feeding rates, we expressed all behaviors as a percentage (arcsine-transformed) of the total min of observation. We analyzed feeding rate as either the total number of trips/h or as the number of trips/nestling/h (=per capita feeding rate). Both the

TABLE 1

RESULTS OF THE MULTIPLE REGRESSION ANALYSIS OF FEEDING RATE (TRIPS/H) FOR KINGBIRD PAIRS IN 1989

Variable	Correlation coefficient (r)	Standardized regression coefficient	Type I F	Type III F
Log (age)	0.623^d	3.848	46.82^d	10.53^c
Precipitation	-0.541^d	-1.534	9.14^c	3.42^a
Nest attendance	-0.521^d	-0.117	2.33	3.32^a
Brood size	0.448^c	1.891	14.42^d	7.22^c
Vigilance	-0.339^b	-0.049	10.81^c	10.81^c
Model $R^2 = 69.3\%$, $F = 16.70$, df = 5, 37, $P < 0.001$				

[a] $0.05 < P < 0.10$, [b] $P < 0.05$; [c] $P < 0.01$; [d] $P < 0.001$; all others not significant.

total and per capita feeding rates were roughly normally distributed. Nestling age was logarithmically transformed in analyses of feeding rate.

We used regression analyses (simple linear and multiple regression) to identify the factors underlying variation in parental behavior. We first examined the strength of the univariate relationships between each dependent variable and all the independent variables. Other behaviors were included as independent variables to examine the potential for trade-offs in parental activities. Variables that were associated significantly ($P < 0.05$) with the dependent variable were then entered into a multiple regression analysis in a sequence corresponding to the strengths of their univariate relationships. We then plotted the residuals against the remaining variables to check for additional relationships. If any were found, the variables were then added to the model. Our objective was to explain the maximum amount of variation in each dependent variable, with the provision that all predictor variables make significant, independent contributions. To assess the significance of each variable, we used the F-values based on the type III sums of squares (SS). Type I SS reflect the impact of each variable as it enters the model, but type III SS measure the significance of each variable only after all the other variables have been entered into the regression model (SAS 1985). For a variable to be retained in the model, we required that its effects remain statistically significant when it was the last variable entered in the model, which meant that the variable had to have a significant type III SS. After the final regression models for feeding rates were determined, we tested for effects of either parental or territory quality by performing an analysis of variance (ANOVA) on the residuals. Unless otherwise noted, significance was established at $P < 0.05$.

RESULTS

Feeding rates.—Age entered the regression first, followed by rainfall, nest attendance, brood size, and vigilance (Table 1). Feeding rate also exhibited significant univariate correlations with cloud cover ($r = -0.373$, $P = 0.01$) and nest cover ($r = 0.442$, $P < 0.01$), but neither had significant type III sums of squares in the regression and were dropped from the model. Thus, feeding rate was positively related to age and brood size but tended to decline as the amount of time spent vigilant increased. The

TABLE 2

RESULTS OF THE MULTIPLE REGRESSION ANALYSIS OF PER CAPITA NESTLING FEEDING RATE (TRIPS/NESTLING/H) FOR KINGBIRDS IN 1989

Variable	Correlation coefficient (r)	Standardized regression coefficient	Type I F	Type III F
Log (age)	0.606[d]	1.051	34.33[d]	4.79[b]
Precipitation	−0.506[d]	−0.935	5.61[b]	7.74[c]
Nest attendance	−0.482[d]	−0.022	1.12	4.25[b]
Brood size	−0.186	−1.012	8.55[c]	12.61[d]
Vigilance	−0.136	−0.038	6.77[c]	6.77[c]
Model R^2 = 60.4%, F = 11.28, df = 5, 37, $P < 0.0001$				

[a] $0.05 < P < 0.10$; [b] $P < 0.05$; [c] $P < 0.01$; [d] $P < 0.001$; all others not significant.

five-variable model accounted for roughly 70% of the variation in feeding rate. The ANOVA comparing the residual variation among the 10 pairs was not significant ($F = 1.30$; df = 9, 33; $P = 0.27$). Thus, none of the unexplained variation appeared to be associated with differences in either parental and/or territory quality.

Although precipitation and nest attendance failed to make significant contributions when entered last (type III SS, Table 1), both were significant ($P < 0.05$) when entered at the last step if the other variable was excluded from the model. In addition, both four variable models explained identical amounts ($R^2 = 0.665$) of the variation in feeding rate. The failure of either variable to achieve significance when both were incorporated in the same model probably stems from the fact that attendance and precipitation were positively correlated ($r = 0.440$, $P = 0.003$). Given that each alone made significant contributions and that our inability to determine which variable was of primary importance, we chose to retain both in the final model (Table 1).

Per capita nestling feeding rates (trips/nestling/h) were correlated significantly with only three of the five variables used in the analysis of total trips/h. In addition to age, precipitation, and nest attendance (Table 2), per capita feeding rates varied with date ($r = 0.302$, $P = 0.05$) and cloud cover ($r = -0.559$, $P < 0.001$), but both variables failed to remain significant in the multiple regression and were dropped from the model. Instead, an examination of the residuals after accounting for age, precipitation, and nest attendance suggested that per capita feeding rates were negatively related to brood size and time spent vigilant. Both of the latter variables were, therefore, entered and retained in the final model and made large contributions (Table 2). Brood size became the most important

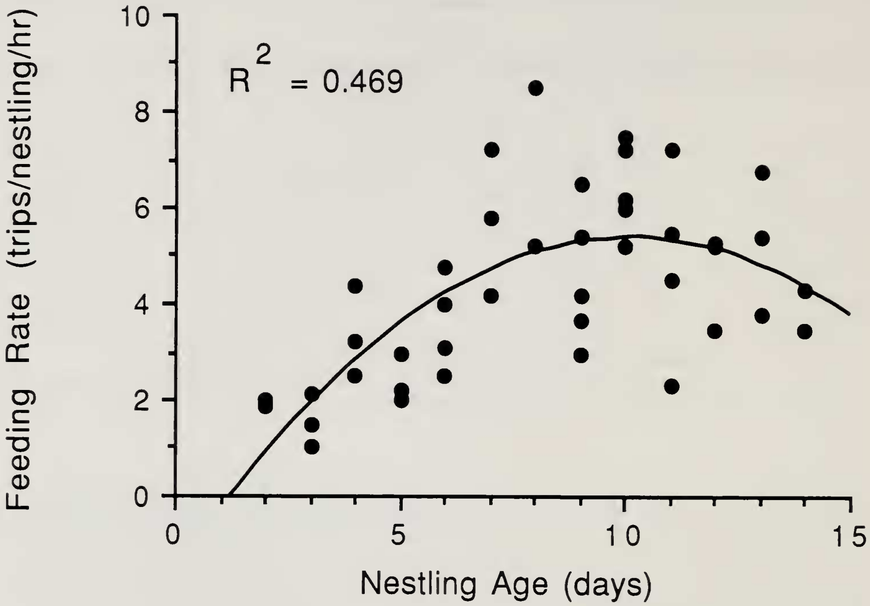

FIG. 1. Per capita nestling feeding rates (trips/nestling/h) plotted against age. The line in the plot is the second-order polynomial described by the formula, FEEDING RATE = −1.63 + 1.387(AGE) − 0.068(AGE^2). Each point represents the average calculated over either a two- or three-h observation period.

determinant of per capita feeding rate, followed by precipitation and vigilance. Overall, the model accounted for 60% of the variation in the number of feeding trips/nestling/h. Residual variation was again unrelated to differences among pairs or territories ($F = 1.0$; df = 9, 33; $P = 0.46$).

That nestling age was of reduced importance in explaining per capita feeding rate (Table 2) was unexpected. The apparent reason was that per capita feeding rate appeared to peak near 10 days of age (Fig. 1). A second-order polynomial explained 46.9% of the variation ($P < 0.001$) in feeding rate. Our results are strikingly similar to data collected by Morehouse and Brewer (1968) from a Michigan population of kingbirds (Fig. 2). Based on the average feeding rate at each age, second-order polynomials accounted for 67.8% and 66.2% of the variation in per capita nestling feeding rate in New York and Michigan, respectively (Fig. 2). In both populations, the predicted maximum feeding rate approached 5.5 trips/nestling/h at either 10 (New York) or 12 (Michigan) days of age. Given this, we reanalyzed per capita feeding rates using the second-order polynomial of age, along with precipitation, nest attendance, brood size,

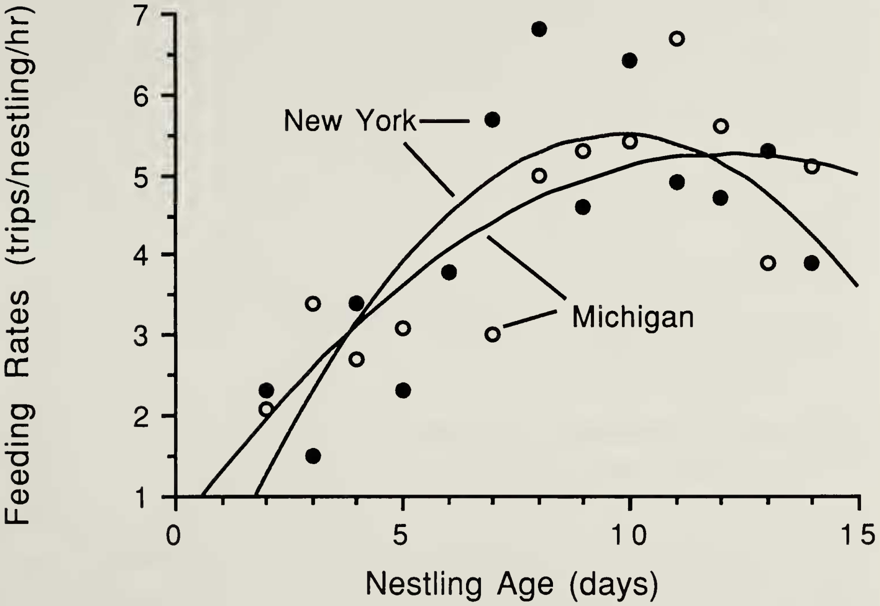

FIG. 2. Average per capita nestling feeding rates by nestling age for the New York study population (solid dots) and a Michigan kingbird population (open circles; from Morehouse and Brewer 1968). Each point represents the mean of 7.5 ± 1.9 h and 7.5 ± 4.67 h of observation in New York and Michigan, respectively. Both curves are second-order polynomials and are described by the following equations: New York, $\mathrm{RATE} = -1.221 + 1.368(\mathrm{AGE}) - 0.070(\mathrm{AGE}^2)$, $R^2 = 0.678$, and Michigan, $\mathrm{RATE} = 0.523 + 0.774(\mathrm{AGE}) - 0.036(\mathrm{AGE}^2)$, $R^2 = 0.662$.

and vigilance. The explained variation increased slightly ($R^2 = 62.4\%$; $F = 11.28$; df = 6, 36; $P < 0.001$), and all of the variables remained significant.

Nestling maintenance.—All analyses of brooding time excluded days 12–14 since kingbirds stopped brooding completely after day 10. Other than age, the other major correlates of brooding were weather variables. Brooding increased as cloud cover ($r = 0.752$) and precipitation ($r = 0.624$) increased and as temperatures fell ($r = -0.564$; df = 34 and $P < 0.001$ for all three). Time spent shading ($r = -0.362$, $P < 0.02$) and total and per capita feeding rates also correlated negatively with time spent brooding (both $P < 0.001$), but the only factor to remain significant, once the affect of nestling age was taken into account, was mean temperature during the observation period (type III SS, $F = 43.95$, $P < 0.001$). Nestlings under 12 days of age were brooded more when temperatures were

TABLE 3

RESULTS OF THE MULTIPLE REGRESSION ANALYSIS OF TIME SPENT VIGILANT (MIN/H) AT NESTS BY KINGBIRDS IN 1989

Variable	Correlation coefficient (r)	Standardized regression coefficient	Type I F	Type III F
Nest cover	-0.455^b	-4.600	13.38^c	7.18^b
Feeding rate	-0.339^a	-1.157	1.52	7.12^b
Nest attendance	-0.176	-0.292	10.73^b	10.73^b
Model $R^2 = 39.7\%$, $F = 8.55$, df = 3, 39, $P < 0.0002$				

[a] $P < 0.05$; [b] $P < 0.01$; [c] $P < 0.001$; all others not significant.

low. Age and air temperature accounted for over 81.1% of the variation in time spent brooding ($F = 69.74$; df = 2, 32; $P < 0.001$).

The amount of time spent shading varied independently of age ($r = 0.163$, df = 41). On average, females shaded young for 6.3 min each hour, but variability was very high ($\bar{x}$ ± SD for percentage of time spent shading 10.6 ± 21.00%). Shading increased when there was little cloud cover ($r = -0.398$, $P < 0.01$) but decreased as brooding time increased ($r = -0.362$, $P = 0.02$) or when air temperatures rose ($r = 0.313$, $P < 0.05$). Of these, only cloud cover remained significant when all three or a combination of any two of the variables was entered into a multiple regression. Plots of the residuals failed to show any trends with other variables. Thus, females shaded young on clear, sunny days.

Vigilance.—The amount of time spent vigilant varied independently of age ($r = 0.108$, df = 41) and averaged 11.4 min/h (19.0% of each hour ± 17.52%). Vigilance tended to be low when nest cover was high ($r = -0.455$, $P < 0.001$) and as the number of feeding trips/h increased ($r = -0.339$, $P < 0.005$). After entry of both variables into the model, we found that residual vigilance was negatively correlated with nest attendance (time spent brooding and shading). The three-variable model of nest cover, feeding rate, and nest attendance explained 40% of the variation in vigilance time (Table 3). After controlling for the effects of these three variables, we found that residual vigilance did not vary with brood size (Kruskal-Wallis test, $H = 2.416$).

DISCUSSION

Activity at the nest was affected by a wide range of factors, only some of which were predictable (e.g., age) or under parental control (e.g., brood size or nest cover). That feeding rates and brooding behavior varied with nestling age was not surprising and has been documented in this (Morehouse and Brewer 1968) and other species (Bedard and Meunier 1983, Best 1977, Breitwisch et al. 1986, Grundel 1987, Johnson and Best 1982, Moreno 1987, Haggerty 1992). Morehouse and Brewer's (1968) and our studies agree in showing that maximum per capita nestling feeding rates average about 5.5 trips per nestling/h and that feeding rate declines towards the end of the nestling period. The decline is temporary, however, since feeding rate nearly doubles about one week after fledging occurs (Morehouse and Brewer 1968). Furthermore, we found that brood size greatly affected nestling feeding rates. Large broods received more feeding trips/h than small broods, but the increase was not sufficient to maintain equivalent rates of feeding to individual nestlings in large broods. Hence, young in large broods were fed less. Differences in parental and/or territory quality did not appear to have an impact on feeding rates since the residual variation from the multiple regressions of total and per capita feeding rates could not be partitioned among nests. This finding indicates that our results were not unduly influenced by conditions at particular nests.

On the other hand, parental behavior was influenced substantially by environmental factors. Precipitation caused feeding rates to drop and low temperatures forced females to brood young. Given that nest attendance was mainly a product of brooding behavior and that nest attendance was negatively correlated with per capita nestling feeding rates (Table 2), weather was clearly an important contributor to variation in the number of times individual nestings were fed. Low feeding rates during inclement weather no doubt resulted from the direct negative effects of precipitation on food availability (e.g., Bryant 1975, Davies 1977) and the indirect effects of low temperature on time spent brooding. This confirms an earlier report (Murphy 1983c) which showed that nestling kingbirds grew poorly and starved frequently when rainfall was high and temperatures were low. Females cannot simultaneously provide adequate food and brood young when weather deteriorates (see also Johnson and Best 1982 and Wittenberger 1982 for similar conclusions for other species). The trade-off between nestling feeding and maintenance suggests a hitherto neglected conflict that may have bearing on the evolution of clutch size. Open-cup nesting species such as kingbirds must surely expend much greater amounts of time and energy maintaining the thermal environment of their nests than do cavity-nesters. The smaller clutch sizes typical of open-cup nesting species (Lack 1968, Martin and Li 1992) may reflect simple constraints on feeding rate and time budgets during thermally stressful periods, rather than differences either in rates of nest predation (Lack 1968, Slagsvold 1982, Lima 1987) or adult survivorship (Martin and Li 1992) between open-cup and cavity nesters.

Finally, the multiple regression analysis of vigilance highlights another important trade-off. Two of the three factors affecting vigilance were other behaviors (nest attendance and per capita nestling feeding rate). Indeed, vigilance time was the second most important correlate of feeding rate (Table 1). Parents must sometimes apparently choose between feeding or guarding young. On the other hand, we found that brood size did not influence the amount of time spent vigilant once we controlled for the effects of parental behaviors and nest cover. This suggests that vigilance was maintained in large broods at the expense of food deliveries.

Kingbirds are known for their vigilant behavior (Smith 1966) and aggressive defense of their nest (Davis 1941, Blancher and Robertson 1982). Smith (1966) noted that males rarely left the nest unattended during female absences. Vigilance presumably improves long distance detection of predators which can then be attacked and kept from the vicinity of the nest. Hayes and Robertson (1989) found a (nonsignificant) trend for widowed female kingbirds to lose more nests to predators than mated pairs. Interestingly, we found that high nest cover was associated with reduced vigilance, suggesting that kingbirds were able to perceive the conspicuousness of their nests and act accordingly. Although in need of further study, the value of aggressiveness and vigilance for kingbirds seems clear. Sacrificing nestling feeding in large broods to maintain vigilance presumably reduces losses of entire broods. Kingbird nests that fail early in the nest cycle are usually replaced, but as the season progresses the probability of renesting following failure declines (Murphy 1983a). Thus, the decision to maintain vigilance over feeding in large broods seems appropriate, given that total nest loss has a much graver impact on seasonal reproductive success than does the loss of an individual nestling to starvation.

Our results show that parental behavior was dynamic and influenced not only by nestling food requirements (as reflected in the correlations with age and brood size) but also by the need to maintain a favorable nest microenvironment and predator-free space. Failure to perform either of the latter two functions may result in complete nest loss to exposure (Murphy 1985) or predation (Murphy 1983b). Consequently, "apparent" food shortage may result from trade-offs in parental behavior, which may have important consequences for the evolution of clutch size and/or nestling growth rate (Lima 1987, Martin 1991).

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